

Review

African cichlid fish: a model system in adaptive radiation research

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The African cichlid fish radiations are the most diverse extant animal radiations and provide a unique system to test predictions of speciation and adaptive radiation theory. The past few years have seen major advances in the phylogenetics, evolutionary biogeography and ecology of cichlid fish. Most of this work has concentrated on the most diverse radiations. Unfortunately, a large number of small radiations and ‘non-radiations’ have been overlooked, potentially limiting the contribution of the cichlid system to our understanding of speciation and adaptive radiation. I have reviewed the literature to identify 33 intralacustrine radiations and 76 failed radiations. For as many as possible I collected information on lake size, age and phylogenetic relationships. I use these data to address two questions: (i) whether the rate of speciation and the resulting species richness are related to temporal and spatial variation in ecological opportunity and (ii) whether the likelihood of undergoing adaptive radiation is similar for different African cichlid lineages. The former is a key prediction of the ecological theory of adaptive radiation that has been presumed true but remains untested for cichlid radiations. The second is based on the hypothesis that the propensity of cichlids to radiate is due to a key evolutionary innovation shared by all African cichlids. The evidence suggests that speciation rate declines through time as niches get filled up during adaptive radiation: young radiations and early stages of old radiations are characterized by high rates of speciation, whereas at least 0.5 Myr into a radiation speciation becomes a lot less frequent. The number of species in cichlid radiations increases with lake size, supporting the prediction that species diversity increases with habitat heterogeneity, but also with opportunity for isolation by distance. Finally, the data suggest that the propensity to radiate within lakes is a derived property that evolved during the evolutionary history of some African cichlids, and the appearance of which does not coincide with the appearance of proposed key innovations in morphology and life history.

Keywords: adaptive radiation; cichlids; ecological speciation; sexual selection; key innovations; species–area relationship

1. INTRODUCTION

One hundred and fifty years after the publication of Darwin’s (1859) book ‘The origin of species’, and after several decades of intensified empirical speciation research (Schluter 2000; Turelli *et al.* 2001; Coyne & Orr 2004) the origin of species remains poorly understood. The importance of divergent selection is now firmly established (Coyne & Orr 2004; Gavrilets 2004), and recent work indicates that speciation driven by divergent selection can be remarkably rapid (Ungerer *et al.* 1998; Hendry *et al.* 2000; Higgie *et al.* 2000; Feder *et al.* 2003). Theory predicts that such ecological speciation is most likely when populations invade new adaptive zones with underutilized niches and may occur in bursts that characterize adaptive radiation (Simpson 1953; Schluter 2000; Dieckmann *et al.* 2004; Gavrilets & Vose 2005). Numerous empirical

studies suggest such conditions may indeed be a common feature of adaptive radiation (Schluter 2000).

Two problems associated with the empirical evidence for rapid ecological speciation as an important source of biological diversity are: (i) quantitative comparative tests of the main theoretical predictions are rare and (ii) most comparative studies ignore the cases where radiation did not take place (but see Bernatchez 2003; Vamosi 2003). Clearly, there are numerous situations where populations failed to radiate despite inhabiting environments apparently conducive to adaptive radiation. Understanding, and being able to predict, when adaptive radiation does and does not occur will perhaps provide the strongest test of theories of ecological speciation and adaptive radiation during the next decade.

The most serious constraint to empirically testing theory is the lack of appropriate model systems. Next to experimental microbial evolution (Rainey *et al.* 2000), the cichlid fish in African lakes are emerging as one of the potentially most powerful model systems in speciation and adaptive radiation research (Kocher 2004). Cichlid fish have radiated into endemic species assemblages in more

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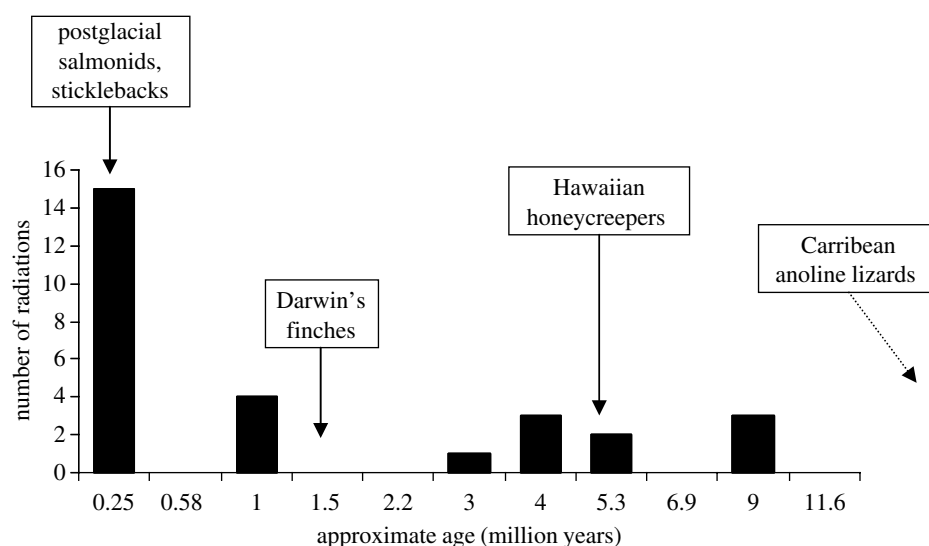


Figure 1. Frequency distribution of the age of African lacustrine cichlid fish radiations contrasted with approximate ages of other well-studied vertebrate adaptive radiations.

than 30 African lakes (table 1 of electronic supplementary material). Between 1000 and 2000 speciation events occurred in the past 5 Myr alone. The large number of independent replicate radiations, their phenotypic diversity, their wide range of ages (10 000 to over 10 Myr; figure 1) and the presence of many more instances where cichlids failed to radiate (table 2 of electronic supplementary material), make this a uniquely powerful model system for empirically testing speciation and adaptive radiation theory.

Inspired by the classic monographs of Fryer & Iles (1972), and Greenwood (1974), effort toward characterizing the nature of cichlid radiations has progressed on multiple fronts, as evidenced by several recent reviews (Stiassny & Meyer 1999; Kornfield & Smith 2000; Seehausen 2000; Danley & Kocher 2001; Markert *et al.* 2001; Turner *et al.* 2001; Kocher 2004; Salzburger & Meyer 2004; Van Alphen *et al.* 2004; Genner & Turner 2005). Simultaneously, speciation research has undergone a transition from verbal models and descriptive empirical work to a quantitative predictive science with strong foundations in ecology (Schluter 2000; Dieckmann *et al.* 2004) and mathematical biology (Gavrilets 2004).

Given these advances, an attempt to integrate cichlid research into the emerging quantitative framework of speciation and adaptive radiation research is timely. To this end, I here explore the environmental and phylogenetic correlates of variation in cichlid speciation propensity. I collected published information on 33 lacustrine radiations with minimum species numbers between 2 and 451 species, and on 76 colonization events without intralacustrine speciation. I use these data to ask why cichlid speciation is sometimes stunningly fast but most of the time not. Even though this is a review, I had to resort to some meta-analysis in the §§3*a,b* and 4.

2. THEORETICAL PREDICTIONS

Two assumptions are pervasive in the cichlid literature. The first is that variation in cichlid speciation rates is explained by ecological opportunity. The second is that a difference between cichlids and other fishes in their propensity to radiate is explained by an evolutionary key

innovation (Nitecki 2000). Ecological opportunity is thought important since most radiations occur following the colonization of lakes. However, that speciation is rapid upon invasion of a new environment does not prove that radiation is driven by ecological opportunity. In organisms with limited dispersal capabilities (like cichlids), colonization of large lakes leads to increased genetic population subdivision and may allow for ecologically neutral population divergence and speciation by drift and sexual selection (Dominey 1984). Indeed several authors have suggested that drift and ecologically neutral divergent sexual selection between isolated populations may drive rapid speciation in cichlids (Ribbink *et al.* 1983; McKaye 1991; Knight & Turner 2004). Adaptive radiation theory (Schluter 2000) and models (Gavrilets & Vose 2005), as well as the extended logic of ecological speciation models (Rosenzweig 1978; Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999), however, make the prediction that after an initial burst speciation rates slow down as niche space fills up. In contrast, speciation driven by niche-independent mechanisms such as non-ecological sexual selection, does not predict such a temporal trend of declining speciation rates in the course of a radiation (although increased extinction rates can generate a superficially similar pattern). Further, consideration of evolutionary and ecological species–area relationships predicts that larger lakes generate more species and allow coexistence of a larger number of species (Losos & Schluter 2000). In the first part of this review, I use published data from 33 African lacustrine cichlid radiations to test these predictions. I arrange the evidence by the nature of the data: distribution of species richness, phylogenetics, population genetics, contemporary evolution.

In the second part, I will compare 33 successful radiations with 76 cases of non-radiation and ask whether they differ in external conditions or phylogenetic history. The evolutionary key innovation hypothesis posits that the invasion of new environments, required for ecology-driven speciation, may be aided by the origin of evolutionary innovations that permit utilization of previously inaccessible niches (Simpson 1953). Liem (1973) and Galis & Drucker (1996) suggested that the functional decoupling of the upper and the lower pharyngeal jaws in cichlid fish is

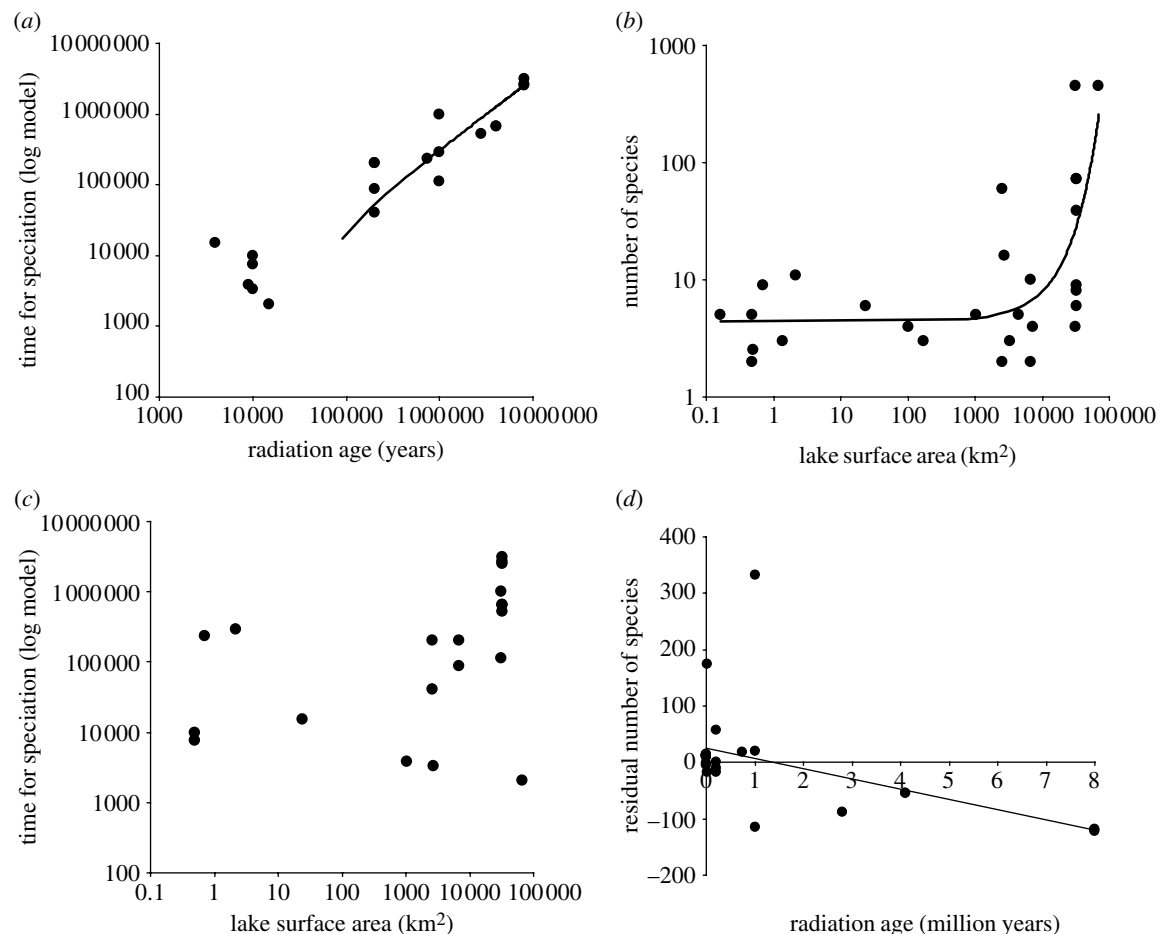


Figure 2. (a) The relationship between time for speciation (TFS) and radiation age calculated using 20 African cichlid radiations for which TFS was available (table 1 of electronic supplementary material). (b) The evolutionary species–area relationship for African cichlid radiations, calculated using 29 African cichlid radiations for which lake surface area and number of species were available (table 1 of electronic supplementary material). (c) The relationship between TFS and lake size calculated using 20 African cichlid radiations for which TFS and lake surface area were available (table 1 of electronic supplementary material). (d) The relationship between residual number of species (after the effect of lake size is taken into account) and radiation age, calculated using 20 African cichlid radiations for which both time in lake and lake surface area were available.

such a key innovation that permitted survival on novel food types through increased behavioural flexibility, and subsequent genetic adaptation to such new resources (West-Eberhard 1989; Galis & Metz 1998). Because for, as far as known, all African cichlids share the decoupled pharyngeal jaw anatomy, if the hypothesis is correct, the high propensity to radiate should be a property of all African cichlid lineages. Salzburger *et al.* (2005) proposed that the parental care behaviour and sexually dimorphic anal fin in one group of cichlids are two key innovations that together allowed for faster divergence by sexual selection. If this was correct, the propensity to radiate should increase concomitantly with the origin of female mouthbrooding and male egg spots.

3. THE DYNAMICS OF SPECIATION RATES DURING ADAPTIVE RADIATION

(a) *Number games: larger lakes generate more species and speciation is fastest when lakes are young*

Most cichlid species of the African lakes are endemic to single lakes. Mitochondrial DNA (mt DNA) genealogies suggest mono- or paraphyly for most lake faunas (e.g. the Lake Malawi and Lake Victoria radiations; Meyer 1993; Nagl *et al.* 2000; Seehausen *et al.* 2003; Verheyen *et al.*

2003) or for large clades within a lake fauna (Lake Tanganyika; Salzburger *et al.* 2002b). It is reasonable in such cases to use the lake's geological age as the maximum possible age for its endemic cichlid radiations, unless molecular clock estimates suggest more recent beginnings for a radiation. Speciation intervals or time for speciation (TFS; McCune 1997) have been calculated that way for all of the larger African cichlid radiations and for several other animal radiations using the number of known extant species (McCune 1997; Seehausen 1999, 2000, 2002, 2005; Turner 1999; Coyne & Orr 2004). One robust result has emerged from these analyses: the shortest average speciation intervals are observed in the youngest radiations (Seehausen 2002).

Here I generalize this result to all known cichlid radiations: I found information on the maximum age ('maximum time in lake', defined as age of lake, or molecular clock estimate of the age of a radiation if less than lake age) for 24 of the 33 radiations. The data are in table 1 of electronic supplementary material. Time for speciation is highly positively correlated with radiation age ($y = 0.32x - 12\,434$, $R^2 = 0.90$, $p < 0.0001$; figure 2a).

I found information on lake surface area for 30 radiations (table 1 of electronic supplementary material). It emerges as a highly significant predictor of species richness across

these radiations ($y = 4.45e^6 \times 10^{-5x}$, $R^2 = 0.47$, $p < 0.0001$; figure 2b), whereas it is unrelated to TFS (figure 2c). The shape of the evolutionary species–area relationship is similar to that observed for the island radiations of anoline lizards (Losos & Schluter 2000) with an important difference: *in situ* speciation of cichlids occurs even in the smallest lakes. The number of species is unrelated to lake size among small and medium sized lakes with between 2 and 11 species, whereas it steeply increases with lake size above 1000 km² surface area. Once the effects of lake size are taken out, residual species richness is significantly negatively related to radiation age: younger radiations contain more species than predicted by lake size ($y = -2 \times 10^{-5x} + 29.94$, $R^2 = 0.29$, $p = 0.009$; figure 2d). This is consistent with the prediction from theory that speciation is fastest early in radiations. It is also consistent with recent empirical (Gillespie 2004) and simulation (Gavrilets & Vose 2005) studies that have documented an ‘overshooting effect’ during adaptive radiation. However, the test cannot discriminate between diminishing speciation and increasing extinction rates. It assumes that the number of extant species is a valid approximation of the number of species that were generated in the course of a radiation. If extinction rates were high, many more species may have been generated, and speciation could be a lot faster. The magnitude of the underestimation of speciation rates would be positively correlated with radiation age, generating a pattern of apparently diminishing speciation rates with increasing radiation age.

Hence, the observed pattern is consistent with diminishing rates of gross speciation as predicted if speciation rates are ecological opportunity-dependent, but also with unchanged speciation rates against a background of increasing extinction rates. Either way, the relationships do imply that both ecological opportunity (net speciation rates decline as an adaptive zone fills up with species) and area size are two important determinants of species richness in the African cichlid fish radiations. The causes of the area effect are likely to be twofold: (i) a positive correlation of area with environmental heterogeneity and hence diversity of niches, (ii) increased opportunity for isolation by distance. To partition the variance contributed by the two components, data on the number of sympatric and parapatric species (alpha diversity) within each lake are required. Such data are currently not available for many lakes. The limited data that are available (e.g. Genner *et al.* 2004), suggest (i) that alpha diversity in large lakes is considerably lower than total species richness (approx. 30% of the latter), implying a large contribution of isolation by distance and (ii) that the shape of the alpha diversity–lake size relationship is similar to that of the species–lake size relationship, implying increased niche diversity contributes to increased species richness in large lakes too.

(b) Tree shape analyses: early speciation bursts and diminishing rates as radiations mature

Changes in net speciation rates through time can be estimated from the lengths of internal branches that separate successive speciation events in a phylogenetic tree. Lineage-through-time plots (Barraclough & Nee 2001) are a way of visualizing such trends. Molecular phylogenies for several African cichlid fish radiations are available for such analysis. If cichlid speciation is driven

and constrained by the availability of vacant niches, we should expect to see the rate of lineage multiplication peak early during radiations and decline as adaptive radiation proceeds.

(i) Young radiations

Absence of mtDNA haplotype lineage sorting, consistent with multiple speciation events in very short succession, characterize every cichlid radiation for which geological or molecular clock age estimates implicated origins within the past 300 000 years: Lake Victoria (Nagl *et al.* 1998, 2000; Verheyen *et al.* 2003), Palaeolake Makgadikgadi (Joyce *et al.* 2005), Lake Natron (Seegers *et al.* 1999) and Lake Ejagham (Schliewen *et al.* 2001). Since speciation is too recent for lineage sorting to have been completed in these radiations, testing for trends in speciation rates within this early phase of radiation is beyond the temporal resolution of mitochondrial gene trees. Species trees can then only be built using large numbers of genomic loci. Clocklike trees built from microsatellite frequency data or Amplified Fragment Length Polymorphisms (AFLPs) are not currently available. However, ultrametric trees for the Lake Victoria radiation (Seehausen *et al.* 2003) confirm that the radiation began as a starburst with very short or no branches separating any two speciation events. However, it is impossible to confirm with existing data whether speciation rates have declined during the course of the radiation.

(ii) Radiations of middle-age

Lake Malawi

Trees based on mtDNA (Meyer 1993; Moran & Kornfield 1993; Kocher *et al.* 1995) suggest the Lake Malawi flock is structured into six well-defined lineages that emerged as an unresolved starburst early in the radiation. The divergence time for these lineages is not well estimated, the lake is 2–5 Myr (ago) old but was largely dry between 1.6 and 1 Myr (ago; Delvaux 1995). It is likely that the six divergent lineages survived this drought. Four of them have radiated further into between 10 and 250 species each, which is thought to have occurred upon lake refilling (Sturmbauer *et al.* 2001). Whereas no haplotype sharing has been observed between any two species from these different lineages (Kocher *et al.* 1995; Parker & Kornfield 1997; Shaw *et al.* 2000; Turner *et al.* 2004), all of the secondary radiations are characterized by lack of haplotype sorting just as the radiations in young lakes (Moran & Kornfield 1993; Parker & Kornfield 1997; Turner *et al.* 2004). Hence, an early radiation burst in Lake Malawi appears to have been followed by a period of stasis and most likely lineage extinction, until renewed radiation bursts in four surviving lineages gave rise to the modern species diversity. Like in the young lakes, these speciation bursts are too recent to detect possible levelling off of speciation rates with lineage-through-time plots using mtDNA gene trees, and ultrametric species-level phylogenies from multilocus data are either not yet available, or cover only a small subclade (Albertson *et al.* 1999; Allender *et al.* 2003).

Lake Barombi Mbo

The lineage-through-time plot for the 0.5–1 Myr old radiation in Lake Barombi Mbo, generated using an ultrametric tree based on genomic AFLP loci (Schliewen &

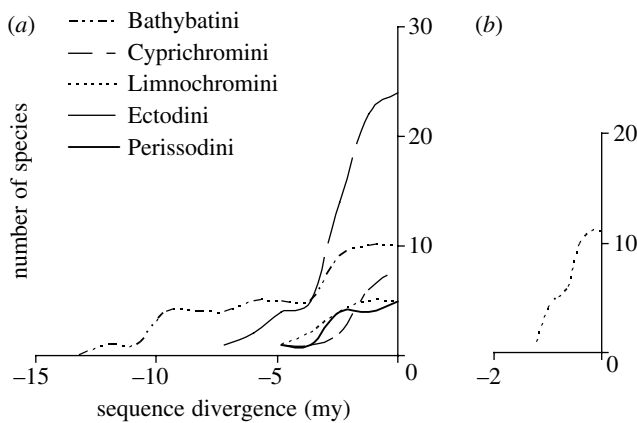


Figure 3. Species number through time plots for African cichlid radiations. (a) Several lineages of Lake Tanganyika cichlids (Limnochromini, Perissodini, Cyprichromini from Duftner *et al.* 2005; Bathybatini from Koblmüller *et al.* 2004, Ectodini from Koblmüller *et al.* 2005). (b) The radiation in Lake Barombi Mbo (Schlieven & Klee 2004).

Klee 2004), suggests an early and a late speciation burst, with a period of stasis following each (figure 3). Trans-specific mtDNA haplotype-sharing is restricted to a single species pair in the second radiation burst, providing additional evidence that speciation rates have recently been low (Schlieven & Klee 2004).

(iii) Old radiations

Where time-intervals between successive speciation events were shorter than required for lineage sorting, the signature of ancient rapid speciation will be preserved in form of polytomies in, and conflict between gene trees. All the major clades in the Lake Tanganyika tree emerged from two such polytomies inferred from mitochondrial genealogies (Salzburger *et al.* 2002) and incongruent short interspersed element (SINE) insertion patterns (Takahashi *et al.* 2001a,b; nodes 2 and 3 in figure 4). The simultaneous origin of all Lake Tanganyika lineages in two major speciation bursts is inconsistent with the hypothesis that the origin of these lineages predates the origin of the lake and they independently colonized the lake from rivers (Nishida 1991; Salzburger *et al.* 2002), but implies instead that the oldest lineages are survivors of an early radiation burst within Lake Tanganyika or a precursor lake basin. Similar to the situation in Lake Malawi, each of these lineages has subsequently radiated into between 6 and 73 extant species, but these radiations are between 2 and 5 Myr old.

I used published linearized trees on five of these radiations (Koblmüller *et al.* 2004, 2005; Duftner *et al.* 2005) for plotting lineages-through-time (figure 3a). All five show evidence of speciation bursts around the same time followed by a period of stasis to the present, although the Cyprichromini show signs of a recent renewed increase in speciation rate (figure 3a). The ancient Bathybatini lineage shows evidence for a much earlier burst as well, and there may have been an earlier burst in the Ectodini. A sixth lineage, the Tropheini, also show evidence of an early starburst followed by declining speciation rates (Sturmbauer *et al.* 2003), even though no ultrametric tree is published that would have allowed a plot. Incomplete lineage sorting seems uncommon among Lake Tanganyika cichlids and when observed among

closely related species has been interpreted, based on distribution data, as evidence of hybridization upon secondary contact (Ruber *et al.* 2001; Salzburger *et al.* 2002). Hence, all evidence suggests that speciation rates have slowed down from the past to the present in Lake Tanganyika.

Short interspersed element analysis allowed the discovery of the oldest burst of speciation in the African cichlid tree as a third area of incongruent SINE insertion patterns (node 1 in figure 4a,b). In this ancient radiation, the precursors of the Lake Tanganyika cichlids, several endemic Congolese lineages, and several now pan-African lineages appear to have emerged simultaneously or in very close succession about 14 Myr (ago), followed by a period of lower speciation (or high extinction) rates (Terai *et al.* 2003). Ultrametric trees that would allow lineage-through-time plots for this part of the African cichlid phylogeny are not currently available. The environmental settings in which this first of the African cichlid radiations occurred have not been investigated. It is tempting to speculate that the radiation happened in an ancient lake that no longer exists (cf. Joyce *et al.* 2005). Time and geographical location make Palaeolake Congo, a large inland sea that existed in the central Congo basin in the Neogene (Cahen 1954), a candidate lake.

(c) Divergent population genetics suggest sustained high speciation rates in sections of the Lake Malawi radiation

Divergent population genetics (Machado *et al.* 2002) hold much promise for studying cichlid speciation. Recent work on some Lake Malawi cichlids suggests that high speciation rates have been maintained in at least one of the four secondary radiations even 0.5–1 Myr after the onset of radiation. Won *et al.* (2005) studied sequence divergence among closely related populations and species of the 'Mbuna' genus *Tropheops* using variation in the number of short-tandem repeats (microsatellites) and linked flanking region sequences (HapSTRs). Estimating divergence times with parameter-rich maximum-likelihood models, they arrived at times since speciation of between 1000 and 17 000 years for the three species studied. Taking a mean speciation interval of 10 000 years as representative for the rock-dwelling Mbuna, the number of 230 extant species in the clade implies that one new Mbuna species arises every 46 years in Lake Malawi (Won *et al.* 2005), a TFS similar to that of the much younger Lake Victoria radiation. These data suggest the speciation rate has remained at 'young radiation levels' 0.5–1 Myr into the Mbuna radiation.

If confirmed, this would implicate speciation mechanisms less closely tied to ecological opportunity than in the tilapiine cichlids of Lake Barombi Mbo and the precursors of the modern haplochromines in the Lake Tanganyika radiation. Mbuna, like Lake Victoria haplochromines, are extremely sexually dimorphic in coloration and very diverse in male colour patterns. It is conceivable that the interaction of drift and sexual selection in subdivided populations is responsible for much of this sustained rapid speciation (Dominey 1984). It is also possible that an interaction between sexual and ecological selection allows a faster and more fine scale response of mating systems to divergent ecological selection (Van Doorn & Weissing 2001; Gavrilets 2004). Won *et al.*'s result requires a high

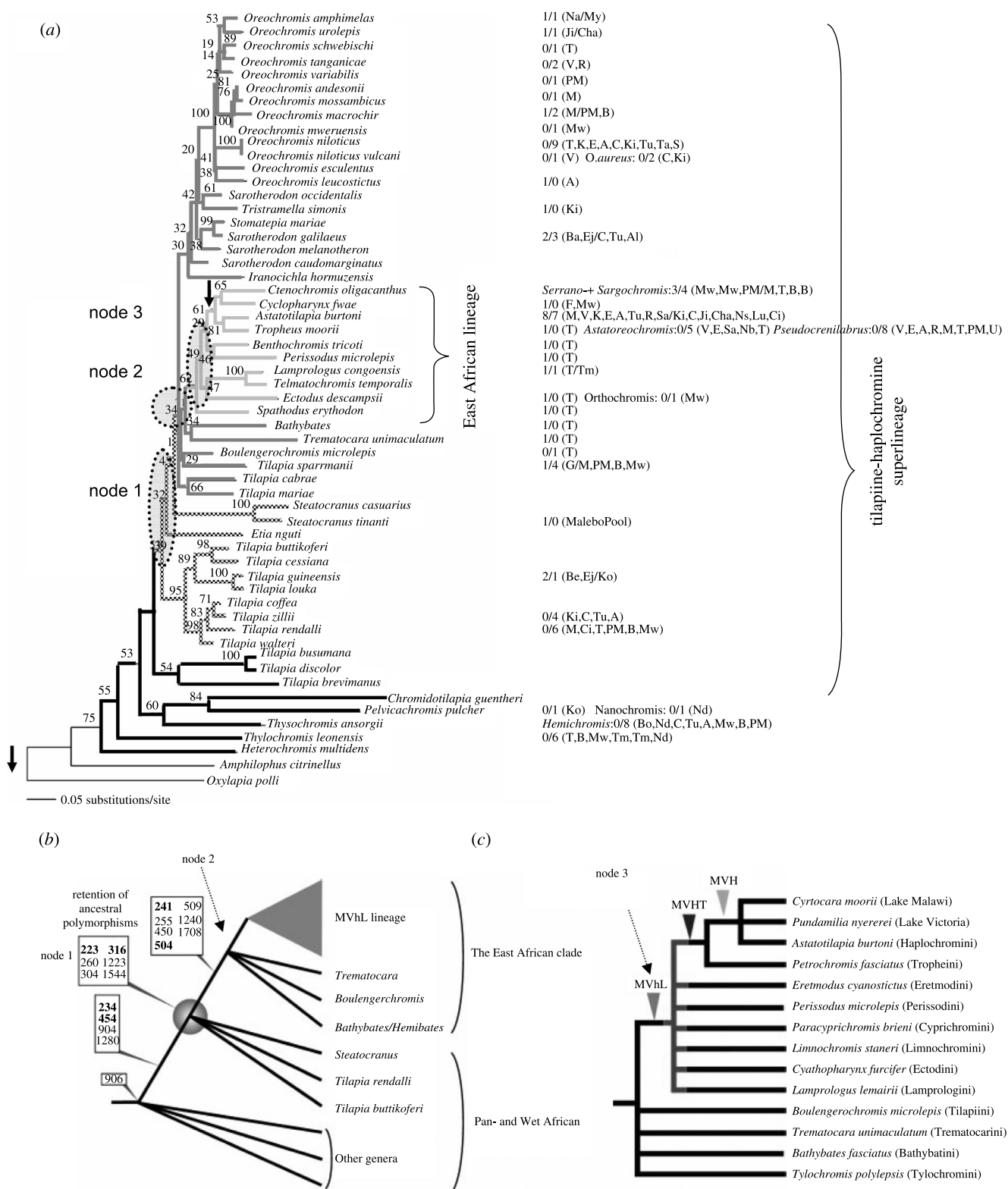


Figure 4. (Caption opposite.)

rate of species turnover in Mbuna. If the radiation of Mbuna began 1 000 000 years ago with the estimated TFS, and has proceeded with steady state rates of speciation and extinction, there may have been 23 000 different species over the years, which is two orders of magnitude more species than we observe in the lake today! How their TFS estimate for *Tropheus* (the most species rich genus of Mbuna) compares to other genera remains to be seen. Many Lake Malawi Mbuna are local endemics with narrow distribution ranges (Ribbink *et al.* 1983;

Genner *et al.* 2004), which is consistent with high-stochastic extinction rates required by the extant richness and TFS estimate.

(d) Adaptive diversification versus reproductive isolation

The widespread combination of (i) a monophyletic mitochondrial genealogy, (ii) starburst-like gene and species trees and (iii) lack of mtDNA lineage sorting can be explained by two scenarios, both of which require some

Figure 4. (*Opposite.*) (a) The ratios of number of successful radiations over number of 'failed' radiations mapped on a mitochondrial gene tree (ND2) for the African cichlid fish (tree from Klett & Meyer 2002). 'Node 1' corresponds to a hard polytomy deep in the African cichlid radiation, that has been interpreted as the signature of an adaptive radiation burst 14 Myr (ago) (Terai *et al.* 2003; figure 4b). 'Node 2' is a second major hard polytomy corresponding with the origin of the four deep lineages of Lake Tanganyika cichlids (Takahashi *et al.* 2001b). 'Node 3' is a third major hard polytomy corresponding to the radiation burst of the modern Lake Tanganyika lineage (Takahashi *et al.* 2001b; figure 4c). Note that several weakly supported nodes in this gene tree collapse to the same polytomy in multilocus trees (figure 4b,c). The different shading indicates sections of the tree that were compared for the ratio of successful to failed radiations. The light grey branch is the 'East African' lineage that emerged in the Tanganyika primary radiation, then radiated again in Lake Tanganyika, and much later seeded Lakes Malawi, Victoria, Makgadikgadi and many others (also figure 4c). Genera that were not sampled for this gene tree, but whose phylogenetic position is known from other mtDNA sequence data, are indicated in the ratio column. Note that the exact position of these does not affect the analysis because all of them are unambiguously assigned to one of the shaded branches. The origins of two proposed key evolutionary innovations, decoupled pharyngeal jaws (at the base of the tree) and egg dummies, are indicated. The third one, female mouthbrooding is not indicated because it evolved multiple times and is scattered throughout the tree. Abbreviations stand for lakes: Na=Naïroba; My=Manyara; Ji=Jipe; Cha=Chala; T=Tanganyika; V=Victoria; R=Rukwa; PM=Paleo-Makgadikgadi; M=Malawi; B=Bangweulu; Mw=Mweru; K=Kivu; E=Edward; A=Albert; C=Chad; Ki=Kinneret; Tu=Turkana; Ta=Tana; S=Stephanie; Ba=Barombi Mbo; Ej=Ejagham; U=Upemba; F=Fwa; Sa=Saka; Ns=Nshere; Lu=Lutoto; Ci=Chilwa; Nb=Nabugabo; Tm=Tumba; G=Guinas sink hole; Be=Bemin; Ko=Barombi ba Kotto; Nd=Mayi Ndombe. (b) A phylogenetic tree based on short interspersed element (SINE) insertion data. Each boxed number is a SINE locus, and arrowheads indicate their origins. The MVhL lineage is resolved in figure 4c. The grey circle at node 1 indicates the period when retention of ancestral polymorphisms (presence or absence of a SINE) was assumed to have occurred at loci 223, 260, 304, 316, 1223 and 1544. Reproduced with permission from Terai *et al.* 2003. (c) A phylogenetic tree for cichlid species in the 12 tribes of Lake Tanganyika, based on SINE insertion data. Arrowheads indicate internodes deduced from insertion of a SINE unit at each of 24 loci analysed. The three clades were supported by the patterns of insertion of a SINE unit at loci 213, 214, 245, 247, 254, 314, 455, 1569, 1666 and 1715 (the MVhL clade); at loci 328, 330, 343, 1221, 1238, 1262, 1269, 1277 and 1654 (the MVHT clade); and at loci 1233, 1265, 1281, 1291 and 1528 (the MVH clade). The grey portion of the tree indicates the period during which extensive putative incomplete lineage sorting of ancestral polymorphisms occurred (reproduced with permission from Takahashi *et al.* 2001b).

non-trivial assumption. In one scenario speciation is concentrated in bursts early during a radiation but begins only after the geographical and demographic expansion of the founding population, in the wake of which the sequence polymorphisms must have arisen that are now still shared between species. This scenario implies a lag between colonization of a lake or newly available habitat (e.g. after a lake level rise) and the beginning of speciation. In this scenario speciation can hence not be simply a by-product of increasing opportunity for isolation by distance. The alternative scenario, that speciation begins during the population expansion (as suggested by Sturmbauer *et al.* 2001), and before the current sequence polymorphisms can have arisen, requires that interspecific hybridization continues for a sufficiently long time after speciation to allow the spread of newly arising mutants across the species, consistent with some empirical observations (Seehausen *et al.* 1997a; Ruber *et al.* 2001; Salzburger *et al.* 2002; Smith *et al.* 2003).

These alternative scenarios have very different implications for the dynamics of the speciation process. Whereas both result in starburst gene trees because all but the divergently selected genes keep coalescing through the entire population, speciation (in the sense of establishment of reproductive isolation) would be rapid in the former, but not in the latter. In the latter only incipient speciation would be fast, but the completion of reproductive isolation would require more time. The hybridization scenario would imply that functional radiation happened in a syngameon situation, as inferred to have occurred in radiations of Darwin's finches (Freeland & Boag 1999), crossbills (Parchman *et al.* in press) corals (Van Oppen *et al.* 2002) and oak trees (Petit *et al.* 2002). This scenario also implies that the divergent natural selection required for adaptive radiation may itself be insufficient to cause completion of reproductive isolation. The latter is

consistent with results of a simulation study of adaptive radiation that found that genomes of species remained 'porous' throughout the radiation (Gavrilets & Vose 2005)

(e) *Contemporary evolution: rapid change is possible*

At least two observations of contemporary evolution in African cichlid fishes suggest rapid incipient speciation may be facilitated by interspecific hybridization associated with environmental perturbation. Lake Victoria experienced major environmental stress beginning in the late 1970s. Loss of water clarity due to nutrient pollution (Verschuren *et al.* 2002) lead to reduced female mate selectivity (Seehausen *et al.* 1997a). Population growth of an introduced top predator (Nile perch, *Lates* spp.) simultaneously caused a crash of cichlid populations (Witte *et al.* 1992). Strongly diminished abundances and impaired vision are probably responsible for the breakdown of reproductive isolation between species. Simultaneously, the ecological resource base and habitat structure underwent major changes too due to eutrophication. After most populations in sublittoral and pelagic habitats had collapsed in the late 1980s (Witte *et al.* 1992), some recovered rapidly in the early 1990s (Seehausen *et al.* 1997b; Witte *et al.* 2000). Among these were populations composed of novel morphological and ecological phenotypes that despite intensive sampling had not been reported prior to the 1980s crash (Seehausen *et al.* 1997b). Some of these phenotypes appear to have been relatively stable since, and may represent incipient species which have arisen within 20 years. The possibility that hybridization contributed to the emergence of these new phenotypes is presently under investigation.

Following translocation from its natural range in northern Lake Malawi to Tumbi West Island in the south in the 1970s, a population of *Cynotilapia afra*

hybridized with resident *Maylandia zebra*, a Mbuna cichlid with different tooth shape but similar male coloration (Streelman *et al.* 2004). Hybridization was first documented in the early 1990s (Stauffer *et al.* 1996); in the following years the hybrid population appears to have expanded its range around the island and within 30 years after the introduction populations from the north and south sides of the island became phenotypically differentiated (Streelman *et al.* 2004). However, it remains to be shown that *C. afra* were not introduced from more than one source population (K. Young 2005, personal communication). Both observations indicate that rapid phenotypic divergence, reminiscent of incipient speciation, is possible following interspecific hybridization.

4. PHYLOGENETIC HISTORY DETERMINES THE PROBABILITY OF ADAPTIVE RADIATION

It is rarely appreciated that the cases in which cichlids radiated are only a minority among all cases in which cichlids successfully colonized lakes in Africa. I use the data on 33 successful and 76 'failed' radiations to ask whether anything is different between the circumstances in which diversification did or did not take place. The answer is there is no difference in either time in lake ($t=0.56$, d.f.=50; $p=0.58$) or lake size ($t=-0.34$, d.f.=80; $p=0.74$). This may be surprising given that the same variables are strong predictors of speciation rate and species numbers in adaptive radiations. Yet, they do not predict whether or not a colonizing population undergoes adaptive radiation.

It is difficult to rigorously test for phylogenetic inertia in cichlid speciation rates because the number of species generated in individual cichlid radiations is often unknown, there are large researcher biases in estimates (Genner *et al.* 2004), all larger phylogenies are highly incomplete, and the level of completeness is generally unbalanced between branches. The phylogenetic distribution of presence and absence of any intralacustrine speciation may under such circumstances be the most robust measure of intrinsic speciation propensity. To test for phylogenetic inertia I mapped lake colonizations with and without intralacustrine speciation onto the only published gene tree of African cichlids that sampled species broadly and without bias towards the large radiations (Klett & Meyer 2002; figure 4a). Although other gene trees may deviate in detail from this one, the overall topology is robust between published African cichlid genealogies.

The occurrence of intralacustrine speciation is not randomly distributed on the tree. All 33 African intralacustrine radiations have occurred within the monophyletic tilapiine-haplochromine superlineage (figure 4a). Although other lineages have Pan-African distributions and colonized many lakes (most prominently the genera *Hemichromis* and *Tylochromis*), they do not appear to have undergone intralacustrine speciation anywhere. Further, *Tilapia*, *Oreochromis*, *Sarotherodon* and the ancient Lake Tanganyika lineages have all given rise to only small intralacustrine radiations, whereas all the large radiations (>10 species) are in the 'East African' lineage.

I used likelihood ratio tests to ask whether the ratios of successful to 'failed' radiations differed between branches of the African cichlid tree. The test detected significant

increases in the ratio from below the polytomy referred to as node 1 in figure 4 to above this and below the second polytomy referred to as node 2 (black versus hatched in figure 4a), from below to above polytomy 2, and from below to above polytomy 3. Within the (light grey) East African branch there was no difference between ratios in the section above versus below the origin of egg spots (figure 4a). Ratios did not differ between the hatched branch (between polytomies 1 and 2) and the grey branches (above polytomy 2), nor between below and above polytomy 2 when the 'East African' branch was excluded, or between the *Oreochromis/Sarotherodon* branch and anything below it. Hence, intralacustrine radiation was significantly more common above than below the deepest major polytomy, independent of an effect of the 'East African' branch, and also significantly more common above than below the second Lake Tanganyika polytomy (polytomy 3).

Hence, the propensity to radiate in response to ecological opportunity is a derived property that accumulated or increased sequentially within the evolutionary history of one lineage among the African cichlids. The decoupled cichlid pharyngeal jaw, although very likely required, was not the key innovation that triggered adaptive radiations in African lakes. Whether its possession affects rates of diversification should be tested by comparing teleost families with and without a decoupled pharyngeal anatomy. Neither maternal mouthbrooding, nor the egg spots on the anal fin of males were required for rapid radiation either. Maternal mouthbrooding is common in many African cichlid lineages, including those that did not radiate in any lake (e.g. *Tylochromis*) but radiation is not confined to mouthbrooding lineages. Egg dummies are confined to the modern haplochromines, a lineage that is nested within a group that possessed high propensity to radiate, even before the origin of egg dummies.

The propensity for intralacustrine speciation increases along one branch in the phylogeny, concomitant with multiple sequentially nested lacustrine radiations. The precursor lineages to all lineages that gave rise to radiations in extant lakes emerged in the wake of an ancient speciation burst 14 Myr (ago) (Terai *et al.* 2003; node 1 in figure 4a,b). Further, the lineage that later gave rise to all the large modern species flocks emerged during a subsequent speciation burst 10 Myr (ago) in one of the lineages that had emerged from the first burst (Takahashi *et al.* 2001a,b; node 2 in figure 4a,b). Finally, the haplochromine lineage that eventually radiated into the unparalleled diversity in Lakes Victoria and Malawi was born within the modern Lake Tanganyika radiation (Takahashi *et al.* 2001b; Salzburger *et al.* 2002, 2005; node 3 in figure 4a,c).

5. CONCLUSIONS

There is evidence for early bursts of speciation in every lacustrine cichlid radiation in Africa for which data exist. Lineage-through-time plots, and the rareness of incomplete lineage sorting among any two species in the older Lakes Barombi (Schliewen & Klee 2004), and Tanganyika (Sturmbauer *et al.* 2003; Koblmüller *et al.* 2004, 2005) and between the lineages of the old primary radiation in Malawi (Parker & Kornfield 1997; Shaw *et al.* 2000) suggest that the frequencies of speciation

diminished in the course of all of the older radiations, even though there appears to have been more than one cycle of burst and stasis in Tanganyika and Malawi, possibly associated with extinction events due to lake level fluctuations. Both lakes shrunk to small fractions of their current size several times in their history (Delvaux 1995; Cohen *et al.* 1997). Importantly, whereas lineage-through-time plots or TFS can only estimate changes in net species accumulation but cannot distinguish between effects of changing speciation and extinction rates, the distribution of lineage sorting in cichlid radiations suggests speciation rates have declined as radiations matured. Consistent with recent numerical simulations of adaptive radiation (Gavrilets & Vose 2005), this suggests the mechanism that makes species number plateau is the diminution of speciation rate rather than increasing extinction rates against a background of consistently high speciation rates. The implication is that speciation itself (not just coexistence) is driven by ecological opportunity, inconsistent with predictions of speciation through drift and ecologically neutral sexual selection. However, it cannot be ruled out that similar patterns might emerge if sexual niche space was genetically (rather than ecologically) constrained such that it will get filled up with time, limiting the opportunity for new species to emerge through sexual selection.

Interestingly, ecological opportunity (the availability of an unoccupied adaptive zone), though explaining rates of diversification in radiating lineages, is alone not sufficient to predict whether a radiation occurs. The available data suggest that the propensity to undergo adaptive radiation in lakes evolved sequentially along one branch in the phylogenetic tree of African cichlids, but is completely absent in other lineages. Instead of attributing the propensity for intralacustrine speciation to morphological or behavioural innovations, it is tempting to speculate that the propensity is explained by genomic properties that reflect a history of repeated episodes of lacustrine radiation: the propensity to radiate was significantly higher in lineages whose precursors emerged from more ancient adaptive radiations than in other lineages.

If the rapid part of adaptive radiations in cichlid fish typically takes place in a syngameon phase in which selection-driven incipient speciation and hybridization interact (Seehausen *et al.* 1997a; Ruber *et al.* 2001; Salzburger *et al.* 2002a,b; Smith *et al.* 2003; Streelman *et al.* 2004) populations may become enriched in adaptive variation at a large number of quantitative trait loci and get rid of genetic constraints. It is likely that only a small fraction of these loci would become fixed upon completion of any one speciation event. Most species would retain much adaptive genetic potential. Such enriched populations may possess an increased propensity to undergo rapid diversification if opportunity arises again.

Further work must aim at identifying differences in genome structure between radiating and conservative lineages to test this hypothesis. Further work is also required to identify the ecological and population genetic causes of variation in speciation rates within and among the radiating lineages. Together, such work will go a long way towards explaining how ecological opportunity and evolutionary history interact to regulate the occurrence and character of adaptive radiation.

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